PROCEEDINGS OF THE

ENTOMOLOGICAL SOCIETY OF WASHINGTON

VOL. 25 DECEMBER 1923 No. 9

A COMPARISON OF THE LABIUM IN CERTAIN HOLOMETABOLOUS INSECTS FROM THE STANDPOINT OF PHYLOGENY.[1]

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Only the elongated, more highly modified types of labium are discussed in the following brief notes, in which I have attempted to establish the homologies of the parts in higher insects; and the present brief discussion will serve as an introduction to a more extensive paper which I have almost completed, dealing with the modifications of the labium throughout the orders of insects, from the standpoint of phylogeny. For the greater part of the material used in the preparation of the present paper, I am greatly indebted to the kindness of Drs. J. M. Aldrich, J. W. Campbell, C. W. Johnson, and A. L. Melander, and I would use this opportunity of expressing my deep appreciation of their generosity which has made this work possible.

The condition exhibited by the bumble-bee shown in Fig. 7, may be taken as the starting point for comparing the parts in the other insects here figured, since the labium of the bumble-bee is as primitive as any of the forms here discussed. In *Bombus*, as is shown in Fig. 7, a basal sclerite called the submentum, *sm*, is followed by an elongated, well developed mentum, *mn*, distal to which are the palpigers, *pgr*, bearing the labial palpi, *lp*. The labial palpi with their palpigers become approximated mesally; thereby displacing the paraglossae, *pgl*, and other parts which become crowded out of their normal position.

In the Coleopteran shown in Fig. 8, the basal sclerite *sm*, apparently represents the submentum *sm* of Fig. 7, and it is possible that the lateral projections "*lo?*" of Fig. 8 may become detached to form the lora *lo* of Fig. 7, although this is not certain. The mentum *mn* is elongated and well developed in the Coleopteran shown in Fig. 8, and is strongly suggestive of the type of mentum *mn* occurring in the bumble-bee (Fig. 7). In the Coleopteran shown in Plate III, Fig. 17, of the paper by Crampton, 1921, the submentum is incorrectly referred to as the "pregula," and the mentum is incorrectly called the "submentum," but in the Coleopterous larva shown in Plate IV, Fig. 27,

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of the same paper, the parts are correctly designated, as in Fig. 5 of the present paper.

The palpigers *pgr* are large and well developed in the Coleopteran shown in Fig. 8, and to the base of each is attached a palpigeral tendon (palpigertendon), similar to those which are familiar to every student who has examined the mouthparts of a beetle in routine classwork in Entomology. The palpigers become approximated mesally, and they comprise the greater portion of the region *pm* of Fig. 8 which was called the prementum by Crampton, 1921, since it is the region immediately in front of the mentum. Due to the mesal approximation of the palpigers *pgr* (with their three-segmented palpi, *lp*), the ligula, *li*, becomes crowded out and is displaced anteriorly. The median portion of the ligula, *li*, probably represents the united glossae, while the lateral portions of the ligula represent the paraglossae which have united with the fused glossae, although the lateral lobes at the tip of the ligula may represent the still distinct terminal portions of the paraglossae.

The Neuropteran shown in Fig. 9 illustrates a slightly higher stage of specialization than that shown in Fig. 8. The distinct submentum *sm* and mentum *mn* of Fig. 8 apparently become united to form the slender columnar structure bearing the labels *sm* and *mn* in Fig. 9. The palpigers *pgr* of Fig. 9 become still more closely approximated mesally than they are in Fig. 8, thereby reducing the area between the palpigers in Fig. 8, which probably represents the remains of the united labiostipites. (For definition of the labiostipes, see paper by Crampton, 1921). The ligula *li* of Fig. 9 is composed largely of the paraglossae, whose lateral portions are bent forward in such a fashion that one can see only the mesal portion of the ligula *li* (composed of the united glossae and paraglossae) in the view shown in Fig. 9.

In the Mecopteran shown in Fig. 10 a still further stage of specialization is reached through the loss of the ligula *li* of Fig. 9, and the reduction of the labial palpi *lp* to two segments. The palpigers *pgr* unite basally, and the region *pm*, or prementum, is composed chiefly of the united palpifers. The slender columnar region bearing the labels *mn* and *sm* corresponds to the region bearing the same labels in Fig. 9, and probably represents the united mentum and submentum.

It is but a step from the condition exhibited by the Mecopteran shown in Fig. 10 to that exhibited by the Dipteran shown in Fig. 11, since in the Dipteran (Fig. 11) the labial palpi *lp* are two-segmented as in the insect shown in Fig. 10, the ligula remains atrophied as in Fig. 10, and traces of the palpiger *pgr* are still retained in the Dipteran shown in Fig. 11, as in the Mecopteran shown in Fig. 10. The slender basal portion of the region proximal to the palpigers *pgr* of Fig. 11 may correspond to the united regions *pm*, *mn* and *sm* of Fig. 10, or the whole

region bearing the labels *pgr* and *pm*, and the proximal parts of Fig. 11, may represent the prementum *pm* alone of Fig. 10. If the latter is the case, the parts have become surprisingly elongated in the Dipteran shown in Fig. 11.

In the flea shown in Fig. 12 the palpi are three-segmented (if I have interpreted Boerner's figure aright), the prementum *pm* is composed of the fused labio-stipes with which the palpigers *pgr* have united, and the region basal to the prementum *pm* represents the mentum *mn*, which, according to Boerner's figure, is demarked from the prementum *pm* in the flea in question. The submentum *sm* is apparently separated from the mentum by a membranous area. In having retained a three-segmented labial palpus, distinct mentum and submentum, the labium of the flea depicted in Fig. 12 is more primitive than that of any Mecopteran or Dipteran I know of, and this may be taken to indicate that the Siphonaptera, or fleas, branched off from the common Mecopteran-Dipteran stem at a phylogenetically early period. At any rate, it would be very difficult to derive the type of labium shown in Fig. 12 from that of any known Dipteran or Mecopteran; and I very seriously doubt that the Siphonaptera are to be derived from the Diptera themselves, and I prefer to derive them from the common ancestors of the Diptera and Mecoptera, although the line of development of the fleas has paralleled that of the Diptera very closely.

I am well aware that the foregoing interpretation of the parts of the labium of the Diptera in particular is quite at variance with that proposed by Peterson, 1916, and again affirmed by Otanes, 1922, who however, exhibits a surprising lack of familiarity with the condition occurring in the Diptera, and in the orders related to the Mecoptera, in his paper on Mecopterous mouthparts; and in criticizing the interpretations of the parts given by Crampton, 1921, it is unfortunate that Otanes did not avail himself of the information given in the paper he attempts to criticize, else he might have avoided many of his mistakes—for which a lack of familiarity with forms related to the Mecoptera is apparently responsible.

Otanes claims that the prementum *pm* of Figs. 3 and 10 is present only in the Mecoptera, and using this as an excuse to discard the term prementum, applied to the sclerite in question in the Mecoptera and allied insects by Crampton, 1921, he dubs the prementum the "mecoglossa." Now the Greek word *mekos* (or *mecos*) signifies *length*, and if the term "mecoglossa" has any meaning at all, it refers to a *long* glossa—but the glossa has become atrophied and utterly disappears in all Mecoptera, so that it is rather amusing to find the appropriate term prementum discarded, and as a substitute for it, to have the term "mecoglossa," signifying "long glossa," applied to a region which has nothing to do with the glossa, in insects in which the

glossa has been completely lost through atrophy! Furthermore, the prementum *pm* is not restricted to the Mecoptera (Figs. 3 and 10), as Otanes would have seen, had he extended his studies to other forms as well as the Mecoptera, since the flea shown in Fig. 12 has a well marked prementum *pm*, the Dipteran shown in Fig. 1 also has a prementum *pm*—as is likewise true of the Dipteran shown in Fig. 4 (where the prementum bears the label *pm*); and in the Neuropteran shown in Fig. 9, and the Coleopteran shown in Fig. 8, the region labeled *pm* (which is composed largely of the palpigers *pgr*) is homologous with the prementum *pm* of the Mecoptera shown in Figs. 3 and 10. Likewise, in the Coleopterous larva shown in Fig. 5, the ligula *li* has become greatly reduced, and the palpigers have united with the fused labiostipites to form the prementum *pm* homologous in every way with the prementum *pm* of the Mecoptera shown in Figs. 3 and 10; so that there is absolutely no basis for Otanes' claim that the prementum (or his "mecoglossa") occurs only in the Mecoptera, and his attempt to substitute the term "mecoglossa" for prementum on these grounds, is as ill advised as his choice of a designation for the structure in question.

Otanes criticizes Crampton, 1921, for designating as the palpigers the structures labeled *pgr* in Fig. 3 of the present paper on the ground that there is supposedly no suture demarking the palpigers *pgr* in *Panorpa lugubris* (Fig. 3), the structures in question being separated merely by a broad, secondarily formed depression, according to Otanes. Otanes claims to have "examined numerous specimens of the labium of *Panorpa lugubris*" without being able to find a suture dividing the palpigers, but if he had looked a little more discerningly he would have discovered that in this insect not merely a suture, but a distinct *cleft*, divides the palpigers *pgr* distally (as shown in Fig. 3), while the basal portions of the palpigers are clearly demarked from the slender median region which represents the united labiostipites, and to the bases of the palpigers are attached the typical palpigeral tendons labeled *pgt* in Fig. 3, which are attached to the bases of the palpigers in the Coleoptera (*Harpalus* and other beetles) and other forms, as is known by every student who has taken a course in insect morphology. If Otanes could not see the huge cleft between the distal portions of the palpigers of *Panorpa lugubris*, however, it is not surprising that he could not see the palpigeral tendons attached to the bases of the palpigers in this insect, either; but the palpigers of *Panorpa lugubris* are none the less clearly demarked, and to their bases are attached the palpigeral tendons which clearly signify their true homologies to any student of comparative anatomy. In this connection, it should be noted that when Otanes writes of the "stipulae" of Panorpa, he does not mean that this insect has pin-feathers, as the term "stipulae" would indicate, but the

structures he refers to are those designated as the labiostipites by Crampton, 1921.

Otanes claims that the mentum *mn* of the Mecopteran shown in Fig. 3 is not the mentum, but is merely the chitinized distal region of the submentum, and for some reason or other the Mecoptera are supposed to have no mentum. I know of no insect, however, in which the submentum occupies the distal position in which the plate *mn* of Fig. 3 is located, and since the sclerite *mn* of Fig. 3 is situated immediately behind the paraglossae *pgl*, is located distally in the posistion characteristic of the mentum of other insects, and is just like the mentum of the sawflies and other Hymenoptera in every respect (see also the mentum *mn* of Fig. 12) I fail to see why it is a detached distal portion of the submentum, especially since the submentum is always reduced in the higher Holometabola, as may be seen in Figs. 12, 8, 7, etc. Otanes has thus again based his criticism upon insufficient data, and a wider knowledge of the insects related to the Mecoptera would have enabled him to form a better founded opinion as to the proper interpretation of the parts of the labium and other head structures in the Mecoptera.

Lastly, Otanes states that "the American species of Mecoptera offer no evidence confirmatory of the opinion" upheld by Crampton, 1917–1921, who maintains that the structures labeled *lp* in the Diptera (Figs. 1, 4 and 11) represent the labial palpi, in opposition to the opinion of Peterson, 1916, who claims that the structures *lp* represent the paraglossae in the Diptera. Here again, a more thorough investigation of the subject might have prevented Otanes from falling into a palpable error, for if one compares the American Dipteran *Empis clausa*, shown in Fig. 11, with any American species of *Bittacus*, such as the one shown in Fig. 10, it is perfectly evident that the labial palpi are slender and two-segmented in the Dipteran (Fig. 11) as in the Mecopteran (Fig. 10), and that the palpi are borne at the apices of palpigers *pgr* in the Dipteran (Fig. 11) as in the Mecopteran (Fig. 10), whereas the paraglossae (*pgl* of Fig. 7) are not two-segmented, and are not borne at the apices of the palpigers (*pgr* of Fig. 10), and in addition, the paraglossae exhibit a marked tendency to become atrophied and disappear completely in the forms most closely related to the Diptera, such as the fleas (Fig. 12) and Mecoptera (Figs. 10 and 3).

Tillyard, 1922, correctly designates the structures labeled *lp* in the Dipteran shown in Fig. 1, as the labial palpi, and I do not know of a better specimen for illustrating that the structures in question are two-segmented labial palpi in the Diptera, than the insect shown in Fig. 1. Furthermore, the fact that in certain Mecoptera the labial palpi exhibit pseudotracheae similar to those occurring on the distal segments (labella) of the labial palpi of certain Diptera (although all Diptera do not have

pseudotracheae on the distal segments of the palpi) clearly indicates that the labial palpi of Diptera are such, rather than paraglossae. In fact, I do not see how any one can compare the parts of the Dipterous labium shown in Fig. 1 with those of the Mecopterous labium shown in Fig. 3 without coming to the inevitable conclusion that the structures labeled *lp* in the Dipteran shown in Fig. 1 are the labial palpi and nothing else, for it so easy to see that the palpigers *pgr* of Fig. 1 are the palpigers *pgr* of Fig. 3, and the two-segmented palpi *lp* of Fig. 1 correspond in every way to the two-segmented palpi *lp* of Fig. 3. If the palpi *lp* of Fig. 1 are the paraglossae, how is it that they are two-segmented (when the paraglossae are not segmented) and are borne at the apices of the palpigers *pgr* in a fashion not occurring in any paraglossae of any known insect? Since no evidence has ever been brought forward to prove that the structures labeled *lp* in Fig. 1 are paraglossae, and since every circumstance clearly indicates that the structures labeled *lp* in Fig. 1 are the labial palpi, the question of the homologies of the labella of the Diptera must be regarded as definitely decided in favor of the view that the labella of the Diptera are the terminal portions of the labial palpi, and unless some actual proof that the labella represent the paraglossae instead, is brought forward in support of the opposite view, further discussion of this question would be merely a waste of time and space which might more profitably be devoted to other subjects.

In several of his papers on the Panorpoid "complex" (a term having nothing to do with psychoanalysis) Tillyard is inclined to place the Mecoptera at the base of the Holometabolous stem, on the basis of the nature of the wings of the Mecoptera. This, however, shows the danger of restricting one's phylogenetic studies to one set of structures alone, since not only are the Coleoptera and Neuroptera more primitive than the Mecoptera in their body structures in general, but even the sawflies (which occupy a position intermediate between the Coleoptera and Neuroptera on the one hand, and the Mecoptera and Trichoptera on the other) are more primitively organized than the Mecoptera in having retained an Orthopteroid ovipositor (lost in the Mecoptera) in the females, and a more primitive type of genitalia (with divided penis valves, etc.) in the males, than is the case with any known Mecopteran. The head capsule and mouthparts of sawflies are much more Orthopteroid, and hence more primitive than these structures are in the Mecoptera; the neck and thoracic sclerites, coxae, legs, etc., of sawflies are of a much more primitive (Orthopteroid) type than are those of the Mecoptera, and the same is true of the abdomen with its appendages—the cerci of a sawfly recently given me by Dr. C. P. Alexander having actually retained the multiarticulate condition occurring in certain primitive Isoptera! Even the wings of

sawflies apparently began their type of specialization at a lower "level" than that of the secondarily homonomous wings of the Mecoptera, since the hind wings of certain sawflies show distinct traces of the primitive Orthopteroid anal fan, which all Mecoptera have lost—so that even on the basis of the nature of the wings, the sawflies are of a more primitive type than the Mecoptera are.

As far as the immature forms are concerned, the larvae of sawflies are much more primitive than those of the Mecoptera in the nature of their head capsules and mouthparts; and the retention of a distinct episternum and epimeron in the thoracic region, together with the long, heavily chitinized (and hence more primitive) coxae, and other parts of the leg, and the more primitive type of abdomen, with jointed stylus-like cerci, etc., (which do not occur in Mecopterous larvae) all point to the larval sawflies as being much more primitive than any known Mecopterous larvae, so far as these characters are concerned. Thus the character of the adults, and most larval features, clearly indicate that the Hymenoptera (sawflies) could not possibly be derived from a Mecopterous type of insect, and what is true of the sawflies is much more so of the Coleoptera and Neuroptera which are more primitive than the sawflies themselves! Tillyard's views in this matter are quite untenable, and the ancestral Holmetabola were doubtless Neuropteroid forms combining in themselves all of the ancestral characters retained by the primitive Hymenoptera, Neuroptera, and Coleoptera.

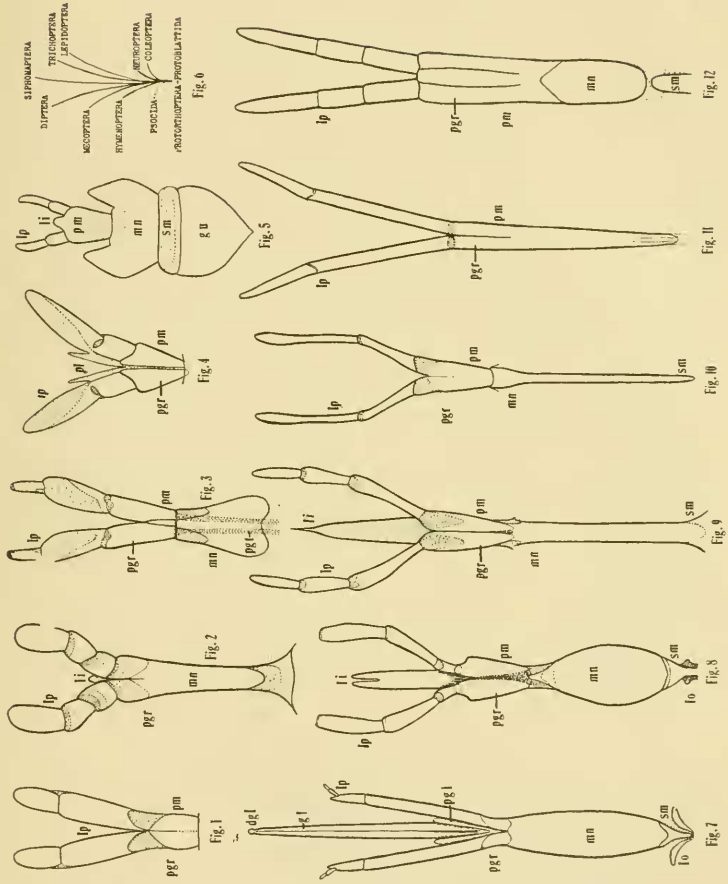
Furthermore, the ancestors of the Holometabola were not the Protorthoptera alone, as Tillyard would maintain, since the lines of descent of the Protoblattida and Protorthoptera both parallel the Holometabola; and the Holometabola were apparently derived from the common Protorthopteran-Protoblattid stem (i. e. the "Prodictyoptera") which had still retained certain Palaeodictyopterous features (certain of which are carried over into the Neuroptera as well) from their common ancestry. The lines of descent of the Holometabola are therefore shown in Fig. 6 as though branching off from the common Protorthopteran-Protoblattid stem, but for the sake of simplicity, the lines of descent of the Isopteroid, Orthopteroid, and Plecopteroid forms which cluster about the base of the Holometabolous stem are not shown in the diagram—although the line of descent of the Psocids, which parallels that of many of the Holometabola, is indicated in the figure, since the Psocids branched off from the common Protorthopteran-Protoblattid stem at the point at which the lines of descent of the Holometabola arose from this same stem.

A study of other parts of the body in general, rather than the labium alone, would indicate that the Coleoptera and Neuroptera are the lowest representatives of the Holometabola (as is

shown in the diagram in Fig. 6), and while the Coleoptera are very closely related to the Neuroptera, they represent a rather aberrant group whose line of descent leads off along its own path of specialization. The Hymenoptera, which occupy a position somewhat intermediate between the Trichoptera and Mecoptera on the one side, and the Coleoptera with the Neuroptera on the other, are as nearly related to the Coleoptera as to any other lower Holometabola (the lower Holometabola are the Coleoptera, Neuroptera and Hymenoptera—and possibly the Strepsiptera also—while the higher Holometabola are the Mecoptera, Diptera, Siphonaptera, Trichoptera and Lepidoptera) and the character of the labium would indicate that the Hymenoptera are closely related to the Coleoptera, and that the Hymenoptera, Coleoptera and Neuroptera are the lowest Holometabolous types.

The tendency for the palpigers (with their palpi) to become approximated mesally occurs in some lower Holometabola (Figs. 7, 8, and 9) as well as in the higher Holometabola (Figs. 10, 11 and 12), and even the tendency for the ligula to become atrophied is exhibited by some lower Holometabola (e. g. Fig. 2), while some lower Holometabola likewise exhibit a tendency for the submentum to unite with the mentum, or for the proximal portions of the labium to become long and slender (as in Fig. 2), so that the principal modifications of the labium of the higher Holometabola are so to speak presaged in the lower Holometabola, which must therefore contain the same tendencies which find opportunity for fuller development in the higher Holometabola. These, and many other features have led me to believe that the usually accepted view that the Holometabola form a natural group is the correct one, despite the fact that I formerly considered that complete metamorphosis might have arisen independently, and that the Holometabola were not necessarily a natural assemblage of insects.

A study of the labium of the higher Holometabola would indicate that the Diptera and Mecoptera are extremely closely related (as is indicated by many other features as well), and that the Siphonaptera are related both to the Diptera and to the Mecoptera, as is shown in Fig. 6. The Trichoptera as well as the Mecoptera have retained many features characteristic of the ancestors of the Diptera, but the labium does not show this as well as might be desired in the material which I have at my disposal, nor does the available material serve to indicate that the Trichoptera are related to the Mecoptera, and parallel the Lepidoptera extremely closely (as indicated in Fig. 6), although I am hoping to obtain the necessary Trichopterous material to fill out the series, in order to complete the study of the labium in all of the orders of insects—which is complete save for the labium of the Trichopterous forms—and I would make use of this



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opportunity to ask that any one who has primitive Trichoptera preserved in fluid, would lend me the desired material long enough to make a sketch of the mouthparts of the insects in question.

References Cited in Text.

Crampton, 1917 A Phylogenetic Study of the Larval and Adult Head of Neuroptera, Mecoptera, Diptera and Trichoptera. Ann. Ent. Soc. America, X, p. 337.

Crampton, 1921 The Sclerites of the Head, and the Mouthparts of Certain Immature and Adult Insects. Ann. Ent. Soc. America, XIV, p. 65.

Otanes, 1922 Head and Mouthparts of Mecoptera. Ann. Ent. Soc. America, XV, p. 310.

Peterson, 1916 Head of Diptera. Ill. Biol. Monogr. 3, No. 2.

Tillyard, 1919 The Panorpod Complex, Pt. 3. Proc. Linn. Soc. N. S. W., XLIV, p. 533.

Tillyard, 1922 Australian Blepharoceridae. Austr. Zool. II, p. 159.

Abbreviations.

dgl —Distiglossa ("labellum" of bee).
gl —Glossa (so called in bee).
gu —Gula.
li —Ligula.
lo —Lora.
lp —Labial palpi (labella of Diptera).
mn —Mentum.
pgl —Paraglossae.
pgr.—Palpigers.
pgt —Palpigeral tendons (Palpigertendons).
pl —Palpal lobes (Palpilobi).
pm —Prementum.
sm —Submentum.

Explanation of Plate XV.

All figures depict the posterior (ventral) surface of the labium.

Fig. 1—Distal portion of labium of Dipteran *Edwardsina*, sp.
Fig. 2—Labium of Coleopteran *Lycus* sp.
Fig. 3—Labium of Mecopteran *Panorpa lugubris*.
Fig. 4—Distal portion of labium of Dipteran *Asyndulum montanum*.
Fig. 5—Labium of larval Coleopteran *Hydrophilus* sp.
Fig. 6—Lines of descent of principal Holometabolous insects.
Fig. 7—Labium of Hymenopteran *Bombus* sp.
Fig. 8—Labium of Coleopteran *Rhipiphorus dimidiatus*.
Fig. 9—Labium of Neuropteran *Nemoptera sinuata*.
Fig. 10—Labium of Mecopteran *Bittacus* sp.
Fig. 11—Labium of Dipteran *Empis clausa*.
Fig. 12—Labium of Siphonapteran (flea) *Pulex serraticeps*, after Boerner, 1903.